

## How many species of fossil arachnids are there?

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**Abstract.** The species-level diversity of fossil Chelicerata is summarized for each order. 1952 valid species of fossil chelicerates are currently recognized, of which 1593 are arachnids. In order of abundance they are: Araneae (979 fossil species), Actinotrichida (283), Eurypterida (241), Scorpiones (111), Xiphosura (96), Trigonotarvida (71), Pseudoscorpiones (38), Phalangiotarvida (30), Opiliones (25), Ricinulei (15), and Anactinotrichida (11). Other groups are represented by ten fossil species or fewer. Based on published descriptions, spiders thus appear to dominate the fossil arachnid species assemblage, making up a greater proportion of paleodiversity than their Recent diversity would predict. Scorpions are also overrepresented, particularly in the Paleozoic, compared to their modern diversity. By contrast, groups like mites, harvestmen, pseudoscorpions and solifuges are noticeably under-represented as fossils when compared to modern patterns of diversity.

**Keywords:** Chelicerata, Arachnida, diversity, fossil, species counts

Harvey (2002: table 1) reported a total – to December 2000 – of 97,682 valid species of Recent Arachnida; with the caveat that many more probably remain to be described. But how many species of fossil arachnids are there? Older figures of 366 valid fossil arachnid species names can be culled from Scudder (1891) and, some sixty years later, Petrunkevitch (1955: 48) had cataloged 505. Since that time there have been important developments in our understanding of arachnid paleontology (see, e.g., Selden 1993). New localities continue to yield new species, while amber spiders (e.g., Wunderlich 2004) have proved to be the major source of new names in recent years. That said, revision of historical types usually lowers diversity once synonyms or erroneously assigned fossils have been recognized. Here, we offer a modern summary of crude fossil arachnid diversity (Table 1) and the most important localities (Table 2) as a baseline for future paleoarachnological research. 1593 valid fossil arachnid species are recognized here from 1776 published names. For completeness we have expanded our review to cover the entire Chelicerata, resulting in a grand total of 1952 valid fossil species from 2283 published names.

### METHODS

No single modern catalog of fossil arachnids and their relatives exists, thus data had to be compiled from various sources as outlined for each group below. Where available, we drew on existing catalogs and/or summary papers, plus additions to the fauna since these publications. Data were cross-referenced to the primary literature wherever possible. Also valuable were lists on Joel Hallan's website <<http://insects.tamu.edu/research/collection/hallan/>>. Here, we restrict counts of valid species to published names and revisions only; i.e., excluding thesis work or papers in progress. The

total number of described names incorporates synonyms, *nomina dubia*, *nomina nuda*, and incorrectly assigned material. For some groups – spiders, mites and the extinct orders in particular – species numbers had to be largely compiled from the primary literature and, due to space limitations, not all sources could be included here in the citations. We eventually hope to produce a more detailed list including taxa, authors, localities, type repositories and references, either as a printed catalog or internet resource. In the meantime the authors are happy to make our provisional lists available on a “fair use” basis upon request.

### RESULTS

**Pycnogonida.**—Nine fossil sea spiders have been described (Poschmann & Dunlop 2006; Charbonnier et al. 2007): one late Cambrian larva from the “Orsten” of Sweden, a Silurian species from the Herefordshire Lagerstätte, UK, four from the early Devonian Hunsrück Slate of Germany and three from the Jurassic of France. Putative fossil sea spiders described from the Jurassic of Germany appear to be misidentified crustaceans.

**“Euchelicerata”.**—An enigmatic Silurian fossil from the Herefordshire Lagerstätte, UK was described as having “chelicerate affinities” (Orr et al. 2000). Since it has opisthosomal opercula – a defining character of Euchelicerata – it can probably be assigned to this clade. Four further species are provisionally listed as “euchelicerates” in our database, but they are primarily there because they are poor fossils of indeterminate affinity.

**Xiphosura.**—Horseshoe crabs are unique among living chelicerates in that there are far more fossil species than the four living ones. That said, the temporal distribution of these species throughout their geological history suggests an overall

Table 1.—Valid fossil species of Chelicerata described to March 2008, divided into geological eras. See text for details of sources. Data includes subfossil (Quaternary: Holocene) occurrences of Recent species, of which 127 involve actinotrichid (oribatid) mites.

| Group                   | Paleozoic | Mesozoic | Cenozoic | Total |
|-------------------------|-----------|----------|----------|-------|
| Pycnogonida             | 6         | 3        | —        | 9     |
| "Euchelicerata"         | 5         | —        | —        | 5     |
| Xiphosura               | 75        | 20       | 1        | 96    |
| Chasmataspidida         | 8         | —        | —        | 8     |
| Eurypterida             | 241       | —        | —        | 241   |
| Scorpiones              | 79        | 16       | 16       | 111   |
| Opiliones               | 7         | 1        | 17       | 25    |
| Phalangiotarbita        | 30        | —        | —        | 30    |
| Pseudoscorpiones        | 1         | 2        | 35       | 38    |
| Solifugae               | 2         | 1        | 2        | 5     |
| Acari: Anactinotrichida | —         | 1        | 10       | 11    |
| Acari: Actinotrichida   | 15        | 15       | 253      | 283   |
| Palpigradi              | —         | —        | 1        | 1     |
| Ricinulei               | 15        | —        | —        | 15    |
| "Pantetrapulmonata"     | 3         | —        | —        | 3     |
| Trigonotarbita          | 71        | —        | —        | 71    |
| Araneae                 | 18        | 31       | 930      | 979   |
| Haptopoda               | 1         | —        | —        | 1     |
| Amblypygi               | 5         | 1        | 3        | 9     |
| Uropygi                 | 6         | 1        | —        | 7     |
| Schizomida              | —         | —        | 4        | 4     |
| all Chelicerata         | 588       | 92       | 1272     | 1952  |
| Arachnida only          | 253       | 69       | 1271     | 1593  |

diversity at any given time in the past similar to that seen today. In earlier studies various Paleozoic fossils vaguely resembling horseshoe crabs were assigned to Merostomata or even Xiphosura. Anderson & Selden (1997) excluded a number of these problematic taxa in their study of Paleozoic Xiphosura. These can be divided into a synxiphosurine stem-lineage and a crown group Xiphosurida; the latter recently shown to extend back to the Ordovician (Rudkin et al. 2008). Data for Mesozoic and Cenozoic xiphosurids are mostly derived from Hauscke & Wilde (1991) and references therein. Currently, 96 xiphosuran species can be recognized, although revisions of Pennsylvanian genera (Anderson 1994, 1997) resulted in quite dramatic reductions in overall diversity. Most species-rich fossil genera appear to be over-split (Anderson 1996), with names based on preservational differences rather than convincing biological features. Further synonyms can be expected and the current total figure is probably an overestimate.

**Chasmataspidida.**—These little-known late Cambrian–mid Devonian marine euchelicerates are characterized by a long postabdomen of nine segments, but share prosomal features with both eurypterids and xiphosurans, rendering their monophyly and affinities uncertain. Seven chasmataspids were listed by Tetlie & Braddy (2004:table 1) and another was added by Poschmann et al. (2005). Both papers include further references and discussions of their morphology and relationships.

**Eurypterida.**—The extinct eurypterids, or sea scorpions, are the most diverse Paleozoic chelicerates. They ranged from the Ordovician to the Permian, with a clear peak of diversity in the Silurian. Tetlie (2007) provided a recent overview of their distribution and phylogeny. Tollerton (2004) proposed that

some 29 Ordovician species are pseudofossils; i.e., sedimentary structures that fortuitously resemble animal material. Excluding these, our provisional list – drawing largely on Tetlie (2004) – documents 241 currently valid eurypterid species names. However, previous workers had a habit of assigning poor-quality specimens to common genera and Tetlie's study suggests that about fifty of these names are potentially synonyms, or otherwise based on non-diagnostic material. Thus, a final figure of c. 190 species may prove more realistic. Further revisions are needed, especially among the families Pterygotidae – which includes the largest recorded arthropods – and Adelophthalmidae, which are common in Coal Measures environments.

**Scorpiones.**—Whereas the fossil record of most (extant) arachnid orders is skewed towards the Cenozoic by large numbers of amber species, the scorpion fossil record is uniquely more diverse in the Paleozoic (Table 1). Drawing on the comprehensive posthumous monograph of Kjellesvig-Waering (1986), Fet et al. (2000) recognized 97 valid fossil scorpion species. Scorpions are the only arachnid order with a well-defined (Paleozoic) stem- and crown-group fossil record. A major question is whether the large number of Mississippian–Pennsylvanian taxa reflects a genuine period of radiation and experimentation – at least three major lineages appear to co-occur during this time – or to what extent this is an artifact of fossil abundance. Kjellesvig-Waering's monograph is problematic in that many Paleozoic specimens were not merely described as new species, but assigned their own family and/or superfamily group. A recent revision by Dunlop et al. (2008) synonymized two Silurian species, and with them eight superfluous higher taxa. Compared to their Paleozoic record, Mesozoic and Tertiary scorpions are quite rare. However, recent work has recovered increasing numbers from amber (Santiago-Blay et al. 2004; Lourenço & Weitschat 2005; and references therein), yielding a current total for all fossil scorpions of 111 valid species.

**Opiliones.**—The harvestman fossil record was reviewed by Dunlop (2007) who recognized 25 valid species and discussed the status of a number of fossils erroneously assigned to this group. The oldest harvestman is a eupnoid from the Rhynie chert and this is followed by a handful of Mississippian and Pennsylvanian species from Europe and North America. A single named Mesozoic example is known from Myanmar (Burmese) amber. The largest species assemblages come from Cenozoic ambers and the Florissant in Colorado, USA. Representatives of all four major lineages (or suborders) have now been found. The putative Pennsylvanian arachnid order Kustarachnida – with effectively only one valid species – is a misidentified harvestman and has thus been included in the Opiliones data. Descriptions of new species from amber are currently in preparation.

**Phalangiotarbita.**—This extinct order ranges from the Early Devonian to the Early Permian and is most common in the Coal Measures of Europe and North America. Petrunkevitch (1953) listed 24 species, plus one dubious taxon (excluded from Table 1); all under the order name Architarbi. There has been no formal revision of this species assemblage, but at least one (lost) fossil managed to get itself named three times which is fairly indicative of the quality of work thus far; see Rößler et al. (2003) for details. A posthumous Kjellesvig-Waering



Table 2.—Significant localities yielding fossil Chelicerata referred to in the text, including details of their stratigraphic position and approximate age in millions of years (Ma). Ages based primarily on the geological time chart of the British Geological Survey <<http://www.bgs.ac.uk/education/britstrat/home.html>>.

| Locality                  | Country                | Period           | Epoch       | Ma      |
|---------------------------|------------------------|------------------|-------------|---------|
| Onyx Marble, Arizona      | USA                    | Neogene          | Pliocene?   | 2–5?    |
| Dominican amber           | Dominican Republic     | Neogene          | Miocene     | 16      |
| Chiapas (Mexican) amber   | Mexico                 | Neogene          | Miocene     | 16      |
| Randecker Maar            | Germany                | Neogene          | Miocene     | 17      |
| Aix-en-Provence           | France                 | Palaeogene       | Oligocene?  | 22?     |
| Florissant, Colorado      | USA                    | Palaeogene       | Eocene      | 34      |
| Baltic amber              | Baltic coast of Europe | Palaeogene       | Eocene      | 44–49   |
| Canadian amber            | Canada                 | late Cretaceous  | Campanian   | c. 78   |
| Sierra de Montsech        | Spain                  | late Cretaceous  | Santonian   | 84      |
| New Jersey amber          | USA                    | late Cretaceous  | Turonian    | 90–94   |
| Myanmar (Burmese) amber   | Myanmar                | late Cretaceous  | Albian      | c. 100  |
| Crato Formation           | Brazil                 | early Cretaceous | Aptian      | 115     |
| Álava amber               | Spain                  | early Cretaceous | Aptian      | 115–121 |
| Lebanese amber            | Lebanon                | early Cretaceous | Nec.–Aptian | 130     |
| Coal Measures             | Europe / N. America    | Pennsylvanian    | Nam.–Steph. | 327–290 |
| Gilboa, New York State    | USA                    | mid Devonian     | Givetian    | 380     |
| Hunsrück Slate            | Germany                | early Devonian   | Emsian      | 390     |
| Rhynie Chert, Scotland    | UK                     | early Devonian   | Pragian     | 410     |
| Herefordshire Lagerstätte | UK                     | Silurian         | Wenlock     | 425     |
| “Orsten”                  | Sweden                 | late Cambrian    | —           | c. 500  |

manuscript mentioned in Selden (1993) proposed a number of synonymies, but was never formally published. Since Petrunkevitch's monographs a few new descriptions have been published, including the oldest record (Poschmann et al. 2005), such that 30 valid species can currently be recognized.

**Pseudoscorpiones.**—Harvey (1991) listed 32 valid fossil pseudoscorpions derived from Myanmar, Chinese, Baltic, and Dominican amber (see also Spahr 1993:12–20). Two further species were treated as *nomina dubia* by Harvey. Also not included as a valid species here is a questionable assignment, listed in Spahr, of a fossil in Romanian amber with affinities to an extant species. Since Harvey's catalogue, we can add the oldest record of the group from the mid Devonian of Gilboa, New York State (Schawaller et al. 1991). This, and further amber records (e.g., Henderickx 2005; Judson 2007), yield a current total count of 38 valid fossil species.

**Solifugae.**—Five fossil camel spider species are known, including a putative stem-group species from the Mississippian of Poland, a poorly-preserved example from the Coal Measures of Mazon Creek, Illinois, USA, one from the Cretaceous Crato Formation of Brazil, and two in Baltic and Dominican amber respectively; see Dunlop et al. (2004) for further details and literature.

**Anactinotrichida.**—Fossil anactinotrichid mites (Parasitiformes in some terminologies) are surprisingly rare given their modern diversity – eleven fossil species in total – and currently have a record no older than the late Cretaceous. They include an opilioacarid from Baltic amber (Dunlop et al. 2004), five named gamasid (or mesostigmatic) species from Baltic and Mexican amber (e.g., Witlański 2000), and five ticks (reviewed by Fuente 2003), mostly from various Mesozoic and Tertiary ambers.

**Actinotrichida.**—Actinotrichid mites (Acariformes in some terminologies) have a much more diverse, and a much older,

fossil record. A putative Ordovician oribatid was not formally named, thus the oldest described actinotrichids come from the Rhynie chert of Scotland and from Gilboa, New York, USA (both Devonian). Further Devonian and Mississippian mites have been recovered from macerates (Subías & Arillo 2002), after which there is a considerable hiatus in the fossil record until mites begin to be formally described again in the mid Mesozoic. Amber is a major source of taxa and Spahr (1993) listed 129 actinotrichids across all ambers. A few amber species have been described since (e.g., Judson & Wunderlich 2003; Norton 2006), while various non-amber sources, like Aix-en-Provence in France (Gourret 1887), contribute to the fossil record too. Taxonomically, the best represented group are oribatids; presumably thanks to their often strongly sclerotized bodies. Their fossil record was reviewed by Krivolutsky & Druck (1986), and Norton (2006) partially revised the Baltic amber species. It is also worth noting that there is an extensive record of subfossil (Holocene) oribatid mites (e.g., Karpinen et al. 1979) from ancient soils and peats only hundreds or thousands of years old. All can be assigned convincingly to Recent species and comprise 127 of the fossil names in our data. Whether they should truly be considered fossils is a moot point, but we have included them in our calculations for completeness. Together with the other (extinct) species this gives a total fossil record of 283 actinotrichid names. Frequent reports of unnamed mites, particularly from various Mesozoic ambers, suggest that this number is a serious underestimate.

**Palpigradi.**—A single, ?Pliocene, fossil palpigrade has been described from the Onyx Marble of Arizona, USA (Rowland & Sissom 1980). A putative record from the Jurassic of Germany is a misidentified insect; see also Harvey (2002).

**Ricinulei.**—Fossil ricinuleids were revised by Selden (1992). All originate from the Pennsylvanian Coal Measures of Europe and North America. Fifteen valid fossil species in

four genera and two families were recognized and no new taxa have been described since.

**“Pantetrapulmonata”.**—Three Devonian arachnid species could not be assigned to any specific order, but were listed – partly for convenience – as probable members of this clade (Dunlop et al. 2006).

**Trigonotarbida.**—This extinct order ranges from the late Silurian to the early Permian and is most common in the Pennsylvanian Coal Measures of Europe and North America. Petrunkevitch (1953) listed 52 valid species – combining data for Trigonotarbida and its synonym Anthracomartida – plus five dubious taxa; at least one of which has since been revalidated (Dunlop & Rössler 2002). There has been considerable movement since Petrunkevitch’s monographs, both in terms of revising older taxa and describing new ones. More remains to be done, especially among the common and clearly over-split Anthracomartidae (see comments in Dunlop & Rössler 2002), but our dataset recognizes 71 currently valid species names.

**Araneae.**—Penney & Selden (2007) provided a brief, general review of the spider fossil record. The oldest example comes from the Devonian of Gilboa, New York, USA (Selden et al. 1991) and a number of Pennsylvanian mesothele-like taxa have been recorded, the affinities of which are currently being revised (P. Selden, pers. comm.). The oldest unequivocal mesothele is late Pennsylvanian and both mygalomorphs and araneomorphs have now been recorded from sedimentary deposits in the Triassic. The vast majority of fossil spiders, c. 820 species, originate from amber. Around 540 species have been recorded from Eocene Baltic amber alone and Wunderlich (2004:203) speculated that three times this number may eventually be recovered from this one deposit. Miocene Dominican amber ranks second with approximately 170 named species (Penney 2006a) and the geographically and stratigraphically contemporary Chiapas (Mexican) amber yields about twenty (e.g., Petrunkevitch 1971). Other Cenozoic ambers – e.g., Parisian (France), Bitterfeld (Germany), Rovno (Ukraine) and China – are beginning to yield spiders too, as are various younger resins or copals; see studies in Wunderlich (2004). Significantly, an increasing number of species have been described in recent years from Cretaceous ambers such as Taimyr, Siberia (Eskov & Wunderlich 1995), Manitoba, Canada, Myanmar (= Burma) (Penney 2006b), New Jersey (Penney 2004a), the Isle of Wight, UK (Selden 2002); Álava (Spain) (Penney & Ortuño 2006) and Lebanese amber (Penney 2003).

Non-amber fossil spiders are much less common, but also derive from a wide range of localities. In addition to the Coal Measures, the most species-rich of these include the Cretaceous of Mongolia and Siberia (Eskov & Zonshtein 1990), Sierra de Montsech, Spain (Selden & Penney 2003), and the Brazilian Crato Formation (Selden et al. 2006). Also significant are the Cenozoic localities of Aix-en-Provence, France (Gourret 1887; Berland 1939), Florissant, Colorado, USA (Petrunkevitch 1922), Shanwang, Shandong, China (Zhang et al. 1994) and the Randecker Maar, Germany (Schawaller & Ono, 1979). Subfossil spiders from peat bogs can also be identified and assigned to extant species (Scott 2003) and these records have been included in our lists. Our total dataset for amber and non-amber spiders yields 979 fossil

species; thus spiders show the highest levels of paleodiversity – approaching three times as many species as the next largest chelicerate groups (Table 1).

**Haptopoda.**—This extinct, monotypic, Coal Measures order was restudied by Dunlop (1999). Its status as a distinct order was confirmed, but no further species have been assigned to it.

**Amblypygi.**—Six species of fossil whip spider are listed in Harvey (2003:22, 30–32), four from the Coal Measures of Europe and North America and two in extant families from Mexican and Dominican amber respectively. Following Harvey, a dubious record from Aix-en-Provence (Gourret 1887) has been excluded. An overlooked Coal Measures name, a new species from the Crato Formation of Brazil (Dunlop & Martill 2002), and one from Mexican amber (Poinar & Brown 2004) bring the total number of currently valid species to nine.

**Uropygi.**—Nine species of fossil whip scorpion are listed by Harvey (2003:73–74, 79–80); and one further Pennsylvanian species was overlooked. Tellie & Dunlop (2008) recognized only six species from the Coal Measures of Europe and North America (one of which may actually be a stem-group schizomid). There is a further species from the Crato Formation of Brazil (Dunlop & Martill 2002), yielding a current total of seven, but a putative species from the Miocene of California, USA is a misidentification.

**Schizomida.**—Four Tertiary species of fossil schizomid in three genera have been described. Three come from the Onyx Marble of Arizona, USA and one from the Oligocene of China. Further details can be found in Harvey (2003:103, 129). No further species have since been recorded, although schizomids from Dominican Republic amber will be described shortly.

## DISCUSSION

Comparing measures of fossil (Table 1) and Recent (Harvey 2002) biodiversity, our species counts imply that the arachnid fossil record is biased in favor of spiders and scorpions. These two orders make up a greater percentage of total fossil diversity compared to their relative abundance in modern ecosystems today. Correspondingly, the fossil record is biased against mites, harvestmen, pseudoscorpions and solifuges. Mites make up almost half of all living arachnid species, but less than a fifth of the fossil paleodiversity. Part of the explanation must be the greater intensity of work on fossil spiders (cf. Wunderlich 2004 and references therein) and to a lesser extent scorpions (Kjellesvig-Waering 1986). By contrast we recognize a corresponding lack of effort, or expertise, when it comes to members of the Acari, Opiliones, Pseudoscorpiones, and the “minor” orders. Physically small taxa, like mites and pseudoscorpions, are generally less likely to be preserved (or noticed). Solifuges tend to be associated today with dry habitats and conditions for fossilization are most favorable where there are substantial bodies of water into which animals can fall and be buried.

It is important to stress that these crude species counts encompass the entire fossil record and to caution against over-interpreting data combined from different time periods and under different conditions of fossilization. Arachnids, and other chelicerates, lack a mineralized exoskeleton, thus their fossil record is sporadic and relies heavily on “windows” of exceptional preservation (Table 2). This makes it difficult to



trace changes in their biodiversity over geological time with any accuracy, since apparent peaks of species-level diversity in the raw data largely reflect productive fossil localities like the Coal Measures or intensively investigated ambers. Nevertheless, superimposing the fossil record onto well-supported cladograms allows the construction of “evolutionary trees.” Since a given taxon must be as old as its sister-group (which may not be preserved) these trees have considerable value in predicting which lineages should have been present during any given time period. They allow quantitative studies of faunal change, such as Penney et al.’s (2003) demonstration that spider families were not affected by the K-T mass extinction event, or Penney’s (2004b) use of richness estimates to show how spider radiations seem to track the radiation of their insect prey over geological time. It is our hope that the raw data we are assembling here can allow similar quantitative studies to be expanded and applied to Chelicerata as a whole.

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